View metadata, citation and similar papers at core.ac.uk

brought to you by

provided by Elsevier - Publish

PERGAMON

Vision Research 39 (1999) 2151–2156

Vision Research

Neuronal responses to plaids

Bernt Christian Skottun *

Skottun Research, 273 Mather Street, Piedmont, CA 94611-5154, USA

Received 30 June 1998; received in revised form 21 October 1998

Abstract

The majority of neurons in the visual cortex are orientation selective. When presented with a plaid, i.e. a stimulus generated by adding two gratings of different orientations, these neurons respond to the individual gratings making up the plaid. However, there are some pattern selective neurons in Area MT of the monkey visual cortex which respond in accordance with the combined plaid. The present study used computer simulation to investigate the response properties of simulated MT neurons to orthogonal plaids. The MT neurons were simulated by first multiplying the outputs of conventional orientation selective V1 neurons and then normalizing the product. It was discovered that pattern selective responses may emerge when the outputs from two orientation selective neurons, which differ in optimal orientation by more than about 50°, are combined in this manner. This demonstrates that pattern selectivity may be the result of a very simple although nonlinear mechanism. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: MT; Model; Plaids; Orientation selectivity

1. Introduction

Neurons in the primary visual cortex are selective for the orientation (Hubel & Wiesel, 1959, 1962) and spatial-frequency (Campbell, Cooper & Enroth-Cugell, 1969; De Valois, Albrecht & Thorell, 1982) of stimuli. When presented with more complex stimuli the majority of neurons respond in accordance with their spatio-temporal spectral receptive field (De Valois, De Valois & Yund, 1979; Movshon, Adelson, Gizzi & Newsome, 1985). That is to say, they respond to the components which fall within the spectral receptive field. These neurons are called 'component selective'. However, some cells in the middle temporal visual area (Area MT) of monkeys visual cortex respond to complex patterns (Movshon et al., 1985). These neurons are said to be 'pattern selective'.

Compared to the primary visual cortex (i.e. Cortical Area 17, or V1) which represents the first-stage of the cortical pathway, the neurons in MT constitute a second-stage of processing (Movshon & Newsome, 1996). ('First-stage' neurons correspond to conventional orientation and spatial-frequency selective neurons in V1, whereas 'second-stage' neurons correspond to cortical neurons which take as their input, either directly or indirectly, the output from first-stage neurons). How the pattern selective properties of second-stage neurons are generated is not clear. Elaborate models have been proposed to account for these properties. Nowlan and Sejnowski (1995) and Sejnowski and Nowlan (1995) used a neural net to simulate pattern selectivity. A problem with neural nets is that, while these models can display remarkable properties, they provide relatively little understanding of the underlying principles. Simoncelli and Heeger (1998) (see also Heeger, Simoncelli & Movshon, 1996) have recently proposed an elaborate model in which MT neurons sum the responses from a large number of first-stage neurons having spectral receptive fields along a constant-velocity plane in 3-D spatio-temporal-frequency space[1]. Whether actual neurons are connected in this manner is not at all clear.

* Tel.: +1-510-658-3246; fax: +1-510-658-3246; e-mail: bernt@best.com.

[1] A 3-D frequency space (as far as visual stimuli are concerned) is made up of two spatial-frequency dimensions and a temporal-frequency dimension. Examples of constant-velocity planes in 3-D frequency space and descriptions of some of their properties can be found in Skottun, Zhang and Grosof (1994)

0042-6989/99/$ - see front matter © 1999 Elsevier Science Ltd. All rights reserved.

PII: S0042-6989(98)00299-5

It is known that cells in Area MT receive monosynaptic input from V1 (Movshon & Newsome, 1996). Since neuronal connections between cortical areas are generally thought to be excitatory the neurons in MT would presumably be integrating excitatory inputs. The present analysis explores multiplication, as an alternative to summation, for combining excitatory inputs. The analysis uses computer simulations to examine the simplest cases of this kind, namely when the output from only two first-stage neurons are combined multiplicatively. Although these cases are extreme in their simplicity, as will be seen, they are capable of generating some interesting response properties.

2. Methods

Receptive fields of first-stage neurons were generated as 2-D Gabor functions so as to resemble cortical simple cells (Jones & Palmer, 1987)[2]. A 2-D Gabor was generated by multiplying a 2-D Gaussian with a sine grating. In order to generate a 2-D spatial-frequency filter the Gabor function was Fourier analyzed and the amplitude spectrum was calculated by computing the absolute of each element in the Fourier series. In order to measure the amount of stimulation reaching each first-stage neuron, the stimulus was filtered through the neurons spatial-frequency filter. To do this, the stimulus was Fourier analyzed and its amplitude spectrum was multiplied, element for element, with the amplitude spectrum of a first-order neuron receptive field. The resulting spectrum of products was summed to give a single value expressing the total amount of stimulation reaching the neuron. The second-stage neuron was simulated by combining the outputs from two first-stage neurons. For the main investigation the outputs were combined multiplicatively. For the purpose of comparison, the outputs were also added. The method was in essence the same as used by Skottun (1998) with the exception that there was no spatial filtering prior to computing the Fourier transform of the stimulus (i.e. Step 2 of that model was omitted).

Throughout the present report the term 'response' is used. The response is assumed to be equivalent to the amount of stimulation. That is to say, the present simulations assumes that the response is proportional to the amount of stimulation.

In order to make it easier to understand the results of the analysis of the first-stage neurons were simulated so as to respond to orientations only over a range of 180°. This corresponds to complete direction selectivity and was achieved by setting equal to zero the amplitudes of the negative components (i.e. the components in the 2nd and 3rd quadrants of the polar plots) in the 2-D spatial-frequency spectrum. This is in agreement with the observation that the input to MT neurons tend to be directionally selective (Movshon & Newsome, 1996).

The computer simulations were carried out on a NeXTStation Turbo (NeXT Computer, Inc) running Mathematica (Wolfram Research, Inc) under NeXTStep (NeXT Computer, Inc).

[2] Although simple and complex cells differ substantially in the space domain their spectral receptive fields are rather similar. Since the present analysis is carried out in the frequency domain, i.e. in terms of spectral receptive fields, both simple and complex cells may serve as first-stage neurons in the present simulations.

3. Results

Fig. 1 illustrates the case where a simulated second-stage neuron combines the outputs from two first-stage neurons which differ in optimal orientation by 30°. The orientation tuning functions for the two first-stage neurons are shown in A. Fig. 1B shows simulated responses to a sine grating of a second-stage neuron which either multiplies (filled symbols) or sums (open symbols) the responses from the two neurons in A. As can be seen, multiplication gives narrower tuning than does addition.

Fig. 1C and D show the responses to orthogonal sine wave plaids. These are plaids which are generated by adding two sine gratings which differ in orientation by 90°. Fig. 1C shows (with filled symbols) the responses to the plaid when the responses from the two first-stage neurons are added. As can be seen this yielded a bi-lobed tuning curve. For comparison Fig. 1C also shows the responses to the two individual components (open symbols). The two lobes in the plaid responses (filled symbols) have maxima at orientations 90° apart and correspond to the case where each component grating is at the optimal orientation for the second stage neuron. This second stage-neuron is obviously component selective.

Fig. 1D depicts second-stage responses simulated by multiplying the outputs from the first-stage neurons. The responses to the plaid are depicted with filled symbols. For comparison (open symbols) the sum of the responses to the individual components are shown. The responses to the combined plaid (filled symbols) have a strongly bi-lobed shape. In fact, the shape is even more pronouncedly bi-lobed than when the inputs were added (i.e. Fig. 1C). The responses to the combined plaid (filled symbols in D) do not differ substantially from the ones obtained by summing the responses to the individual components (open symbols in D). There can be little doubt that this simulated second-stage neuron is component selective.

An important feature of the model is normalization of the responses. In the present case the tuning curves were normalized by scaling the responses so that the

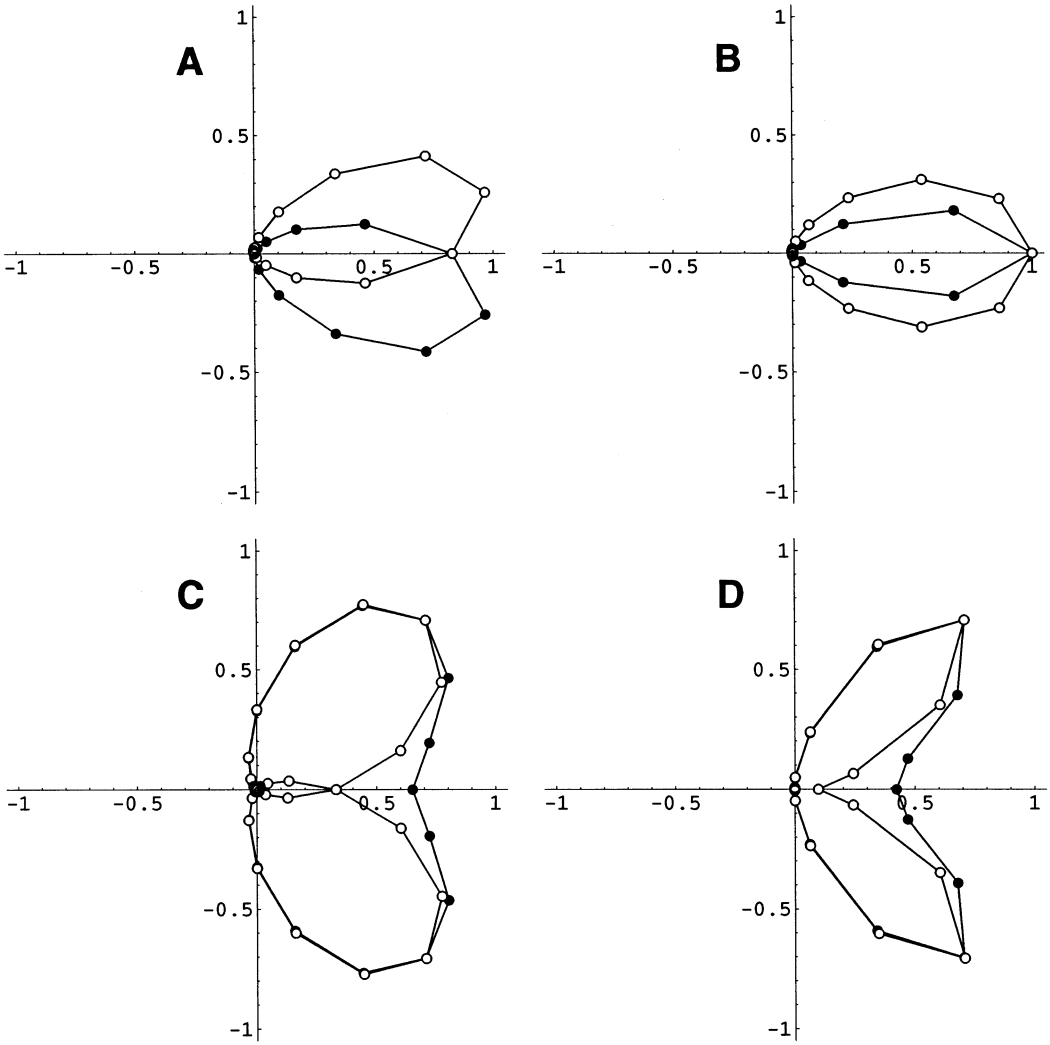

Fig. 1. The orientation selectivity (in polar coordinates) of first-stage neurons and of second-stage neurons simulated by combining their outputs. (A) The orientation selectivity of two first-stage neurons. One neuron is represented with open symbols and the other with filled symbols. The two neurons differ in optimal orientation by 30°. Each first-stage neuron had an orientation tuning width (half-width at half-height) of approximately 30°. 'First-stage neurons' correspond to conventional orientation and spatial-frequency selective neurons as are commonly found in the primary visual cortex of cats and monkeys. (B) The responses of two second-stage neurons to sinusoidal gratings. One neuron (open symbols) was simulated by adding the outputs from the two first-stage neurons. The other neuron (filled symbols) was simulated by multiplying the outputs. (C) The responses to plaids of a second-stage neuron generated by adding the outputs from the two first stage neurons in panel A. The filled symbols indicate the responses to an orthogonal sine wave plaid. The open symbols depict the responses to the individual components making up the plaid and are essentially rotated versions of the graph (open symbols) in panel B. The filled symbols represent the sum (at each orientation) of the open symbols. Because the responses to the plaid are the sum of the component responses, a second-stage neuron simulated in this manner is component selective by definition. (D) The responses to orthogonal plaids of a second-stage neuron which combines multiplicatively the outputs from the two first-stage neurons in panel A. Filled symbols represent the responses to the combined plaid while open symbols depict the sum of the responses to the two components presented separately. As is apparent, the combined responses (filled symbols) are quite similar to the sums of the component responses (open symbols). This neuron is therefore clearly component selective. (All tuning curves have been normalized by scaling so that the highest response in each curve equals 1.0.)

largest response in each curve equals 1.0. Normalization is a relatively standard feature in models of cortical connectivity (e.g. Heeger, 1991; Heeger et al., 1996) and serves to ensure that a neuron operates within its dynamic range. Normalization is most commonly thought to be accomplished through intracortical inhibition, the presence of which is well established at least in the primary visual cortex of cats (Sillito, 1975; Ferster, 1986; Ramoa, Shadlen, Skottun & Freeman, 1986).

Fig. 2 depicts the case where the two first-stage neurons differ in orientation by 60°. The pair of first-stage neurons are shown in A. The second-stage responses to sine gratings are depicted in B where open and filled symbols depict responses generated by, respectively, adding and multiplying the outputs from the two first-stage neurons. As was the case in Fig. 1, multiplication (filled symbols) yields the narrower tun-

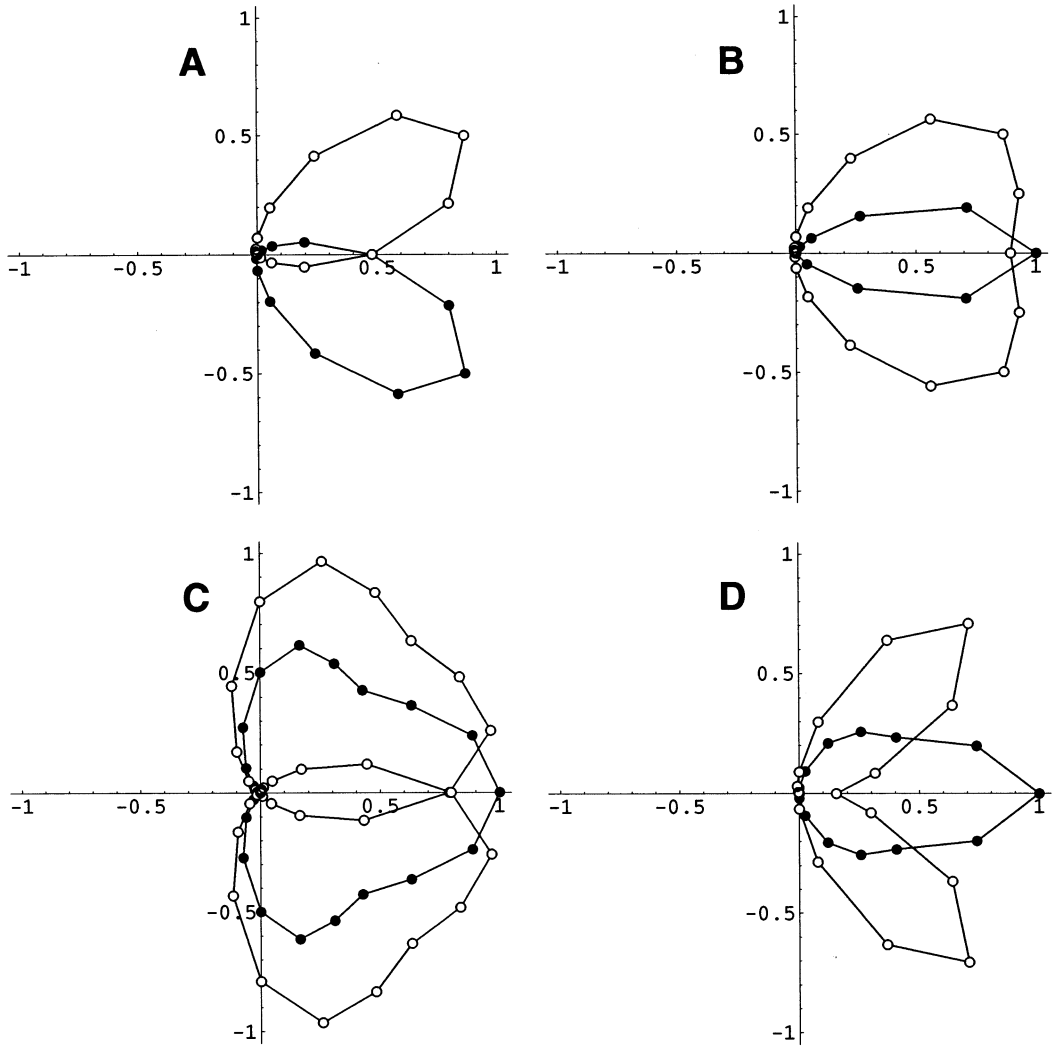

Fig. 2. The same as Fig. 1 with the exception that the first-stage neurons (A) differ in optimal orientation by 60°. In the case of a second-stage neuron which sum inputs (panel C) the plaid responses (filled symbols) may appear to fall somewhere between pattern and component responses. However, since the plaid responses can be generated by summing (and normalizing) the component responses, the neuron has to be characterized as component selective. On the other hand when the inputs are multiplied (D) the plaid responses (filled symbols in D) show clear pattern selectivity.

ing. Fig. 2C and D depict the responses to plaids (filled symbols) generated by adding (C) and multiplying the inputs (D). In the case of addition (i.e. Fig. 2C) the plaid responses are somewhat narrower than the responses to the two components (open symbols). The neurons simulated in this manner are clearly not pattern selective since the plaid responses are the sums of the component responses. (The responses therefore satisfy the definition of component selectivity.) On the other hand, when the outputs are multiplied (Fig. 2D) the responses to the combined plaid (filled symbols) are fundamentally different from the responses to the components (open symbols). In this case the responses to the plaid cannot be generated by summing the responses to the component gratings. The neuron in Fig. 2D is pattern selective since the optimal orientation to the plaid (Fig. 2D, filled symbols) is the same as the optimal orientation for a single grating presented alone (Fig. 2B, filled symbols). That is to say, the peak response to the single grating occurs at an orientation which differs by 45° from the optimal orientations of each of the component gratings when these are presented together in the plaid.

4. Discussion

The present simulations have demonstrated that second-stage neurons which multiply the inputs from pairs of orientation selective first-stage neurons may display pattern selectivity provided the two first-stage neurons differ sufficiently in optimal orientation. Further analyses using orthogonal plaids revealed that neurons need to differ in optimal orientation by approximately 50° or

more in order to show pattern selectivity. On the other hand, combining the outputs from pairs of first-stage neurons having optimal orientations differing by less than about 40° will yield component selective behavior. In the range of 40–50° neurons show behavior that is intermediate between component and pattern selective. If one hypothesized that second-stage neurons may vary more or less continuously with regard to differences in optimal orientations among their input cells, then one might expect them to vary in a continuous manner with regard to pattern versus component selectivity. This appears to be what Movshon et al. (1985) observed in Area MT of the monkey. The present analysis may therefore provide a very simple, although non-linear, mechanism, which not only accounts for pattern selectivity, but also accounts for the variability among MT neurons with regard to this property.

Multiplication of neuronal inputs can be brought about by a number of different neural mechanisms (Koch & Poggio, 1992) and is consistent with the fact that MT neurons have steeper contrast response functions than V1 neurons (Sclar, Maunsell & Lennie, 1990). Furthermore, the higher degree of direction selectivity among MT neurons as compared to V1 neurons (Van Essen, Maunsell & Bixby, 1981; Maunsell & Van Essen, 1983; Albright, 1984; Albright, Desimone & Gross, 1984) is compatible with multiplicative integration. This can be understood very simply by considering the case of two first-stage neurons which both respond twice as strongly to drift to the right than to the left. A second-stage neuron multiplying the outputs from these two neurons would then respond four times as strongly to rightward movement than to movement to the left, thereby creating a higher degree of direction selectivity in the second-stage neurons. (The same general principle could also enhance selectivity for other stimulus parameters.)

It has recently been shown that multiplication of output from orientation selective neurons may create end-stopping in second-stage neurons (Skottun, 1998). The conditions which favor pattern selectivity in the present analysis are similar to the ones which produced end-stopping in the earlier study. This seems to suggest that there may be a connection between end-stopping and pattern selectivity. The findings that MT neurons respond very well to both single dots and to patterns of random dots (Albright, 1984; Albright et al., 1984) is consistent with this suggestion. [Single dots and patterns of random dots have similar amplitude spectra and differ mainly in their phase spectra. Thus one would expect to find a high correlation between the responses to single dots and patterns of random dots. This appears to be the case for actual MT neurons (Albright, 1984) and suggests that the neurons respond in accordance with the amplitude spectra (as opposed to the phase spectra) of the stimuli. This lends credence to the present approach, which is based on amplitudes]. This is obviously a topic in need of further exploration.

The present analysis is carried out in terms of spatial tuning. In fact, it is primarily based on orientation selectivity. The analysis does not deal with temporal factors such as movement and drift direction, etc. (The fact that the neurons were simulated as fully direction selective was mainly out of convenience so as to make the polar-plots clearer.) Movshon et al. (1985) characterized the difference between component selective and pattern selective cells in terms of direction, i.e. pattern-direction-selective versus component-direction-selective neurons. The fact that the present analysis has generated pattern selectivity from purely spatial characteristics suggests that pattern selectivity needs not be a feature of the responses to movement. It is generally desirable to account for phenomena using the lowest possible number of terms. The present results therefore suggest that it may be possible to simplify the analysis of pattern selectivity by accounting for this property without temporal factors[3]. This should not be taken to imply that the neuron generated in this manner would not display pattern-direction-selectivity. They certainly would. That is to say, provided the input to these neurons is from directionally selective neurons. What the present analysis has shown is that direction selectivity need not be involved in the mechanism whereby pattern selectivity is generated.

Based on the present results one can suggest a possible model for pattern-direction-selectivity in MT. In this model direction selectivity is mainly a feature passed on from V1. Consistent with this view is Movshon and Newsome's (1996) observation that the neurons in V1 which project to MT tend to show a very high degree of direction selectivity. At a second stage, inside Area MT, pattern selectivity is generated by multiplication. In this model, pattern selectivity and direction selectivity stem from what are essentially (with the minor qualification, as pointed out above, that multiplication may sharpen direction selectivity) two independent mechanisms.

The present study has focused on summation and multiplication because these two operations describe excitatory connections[4]. It is generally believed that neurons whose axons travel from one cortical area to another are excitatory and that inhibitory connections are largely confined to local interactions within any

[3] This, of course, does not mean that there may not be other reasons for taking movement and time into account. Nor should it be taken to mean that one should not be using moving stimuli when mapping out the response properties of MT neurons.

[4] A feature of multiplication is AND-gating. Multiplication creates gating of this kind because the product of two numbers is zero if either number is zero. This suggests that it may be possible to generate pattern selectivity with other models based on AND-gating.

given cortical area. Therefore, a cortical neuron integrating inputs coming directly from outside its own cortical area would most likely be receiving excitatory inputs. This does not mean that these neurons could not also be receiving substantial inhibitory inputs of local origin. The present simulations have largely disregarded this case (except for the assumption that response normalization may be the result of inhibition), not because it is improbable, but because the goal was to examine the simplest possible case and to try to understand what can be achieved with some very simple arithmetic operations. It seems that it is only after one has understood what can be achieved with the simplest operations that one is in a position to determine what further factors need to be invoked to account for actual neuronal behavior. By examining a very simple case, the present simulations have demonstrated that multiplication by itself may be sufficient to account for pattern selectivity in second-stage neurons.

References

Albright, T. D., Desimone, R., & Gross, C. G. (1984). Columnar organization of directionally selective cells in visual area MT of the macaque. *Journal of Neurophysiology*, *51*, 16–31.

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology*, *52*, 1106–1130.

Campbell, F. W., Cooper, G. F., & Enroth-Cugell, C. (1969). The spatial selectivity of the visual cells of the cat. *Journal of Physiology* (*London*), *203*, 223–235.

De Valois, K. K., De Valois, R. L., & Yund, E. W. (1979). Responses of striate cortex cells to gratings and checkerboard patterns. *Journal of Physiology* (*London*), *291*, 483–505.

De Valois, R. L., Albrecht, D. G., & Thorell, L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Research*, *22*, 545–559.

Ferster, D. (1986). Orientation selectivity of synaptic potentials neurons in of cat primary visual cortex. *Journal of Neuroscience*, *6*, 1284–1301.

Heeger, D. J., Simoncelli, E. P., & Movshon, J. A. (1996). Computational models of cortical visual processing. *Proceedings of the National Academy of Sciences*, *93*, 623–627.

Heeger, D. J. (1991). Nonlinear model of neural responses in cat visual cortex. In M. S. Landy, & J. A. Movshon, *Computational models of visual processing* (pp. 119–133). Cambridge, Massachusetts: MIT Press.

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology* (*London*), *148*, 574–591.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology* (*London*), *160*, 106–154.

Jones, J., & Palmer, L. (1987). An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex. *Journal of Neurophysiology*, *58*, 1233–1258.

Koch, C., & Poggio, T. (1992). Multiplying with synapses and neurons. In T. McKenna, J. Davis, & S. F. Zornetzer, *Single neuron computation* (pp. 315–345). Boston, Massachusetts: Academic Press.

Maunsell, J. H. R, & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, *49*, 1127–1147.

Movshon, J. A., Adelson, E. H., Gizzi, M. S., & Newsome, W. T. (1985). The analysis of moving visual patterns. In C. Chagas, R. Gattass, & C. Gross, *Pattern recognition mechanisms* (pp. 117–151). The Vatican: Pontificia Academia Scientiarum.

Movshon, J. A., & Newsome, W. T. (1996). Visual response properties of striate cortical neurons projecting to area MT in macaque monkeys. *Journal of Neuroscience*, *16*, 7733–7741.

Nowlan, S. J., & Sejnowski, T. J. (1995). A selection model of motion processing in area MT of primates. *Journal of Neuroscience*, *15*, 1195–1214.

Ramoa, A. S., Shadlen, M., Skottun, B. C., & Freeman, R. D. (1986). A comparison of inhibition in orientation and spatial frequency selectivity of cat visual cortex. *Nature*, *321*, 237–239.

Sclar, G., Maunsell, J. H. R., & Lennie, P. (1990). Coding of image contrast in central visual pathways of the macaque monkey. *Vision Research*, *30*, 1–10.

Sejnowski, T. J., & Nowlan, S. J. (1995). A model of visual motion processing in area MT of primates. In M. S. Gazzaniga, *The cognitive neurosciences* (pp. 437–449). Cambridge, Massachusetts: MIT Press.

Sillito, A. M. (1975). The contribution of inhibitory mechanisms to the receptive field properties of neurones in the striate cortex of the cat. *Journal of Physiology* (*London*), *250*, 305–329.

Simoncelli, E. P., & Heeger, D. J. (1998). A model of neuronal responses in visual area MT. *Vision Research*, *38*, 743–761.

Skottun, B. C., Zhang, J., & Grosof, D. H. (1994). On the directional selectivity of cells in the visual cortex to drifting dot patterns. *Visual Neuroscience*, *11*, 885–897.

Skottun, B. C. (1998). A model for end-stopping in the visual cortex. *Vision Research*, *38*, 2023–2035.

Van Essen, D. C., Maunsell, J. H. R., & Bixby, J. L. (1981). The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties and topographic organization. *Journal of Comparative Neurology*, *199*, 293–326.